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SOME GENERAL RESULTS OF RECENT NORWEGIAN RESEARCH WORK ON ARCTIC LICHENS¹

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(Plates 284 and 285)

IN 1921 the writer joined the Norwegian scientific expedition to Novaya Zemlya. The botanical results have been published by the Norwegian Academy of Science in Oslo. In 1926 he worked in Spitsbergen (Bell Sound). His large collections from this expedition have in part been determined, but the results have not yet been published. In 1929 he worked in North East Greenland as a member of the expedition, which the Norwegian Svalbard-og Ishavs-under-søkelse (the "Svalbard Office") equipped.

In addition to his own collections he has also (entirely or in part) determined the Arctic lichen collections of Th. M. Fries from Bear Island and Spitsbergen in 1868 and from West Greenland in 1871, and he has determined the lichens from several Norwegian expeditions to the Svalbard region and to East Greenland. Together with his friend P. F. Scholander he has worked up Scholander's lichen collections from North East Greenland from the Norwegian expedition of the year 1930. He has also had full access to the large Arctic lichen collections in Copenhagen (from Greenland), Helsingfors (Bering Strait), Stockholm (Spitsbergen and Eastern Siberia), and Upsala (Spitsbergen).

Compared with these Scandinavian herbaria the Arctic lichens of the other herbaria in the world are less important. And they are not

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always accessible, for several important herbaria have rules that restrict the loan of their material to other institutions.

As a result of these studies he has arrived at some general results on the distribution of Arctic lichens, which he would like to present to an American public. For they imply some suggestions on the little known lichen flora of the North American high mountains, especially on the nivale lichen flora of the Rocky Mountains.

Let us first consider the lichen flora of North East Greenland, from Scoresby Sound and northwards. The Second German Polar Expedition in 1870-71 was the first to collect lichens here. The expedition worked under extreme difficulties in this region, which was then very little explored. It was in reality almost unknown. Their lichens were determined by the German lichenologist G. W. Koerber, who identified 52 species in the collection. The next botanist on the area was the Danish Dr. N. Hartz in 1891. He chiefly worked in Scoresby Sound, about 70° - 72° N., south of the German field of exploration. Dr. Hartz's very important paper, which has, perhaps, not been duly appreciated, contains interesting observations on the vegetation, the importance of the snow cover, and also on the lichens. His lichen results were remarkable. Deichmann Branth identified 190 species in his collections. During the Danish expedition in 1898-1902 Ch. Kruuse collected a few lichens near the outlet of Scoresby Sound, and especially in the Angmagsalik district, south of Scoresby Sound, about 66° N. His scientific interest was the vascular plants. The Swedish Nathorst expedition in 1899, in search of the aviator Andrée, completed our geographical knowledge of the large fjord system north of Scoresby Sound, now called Eirik Raude's Land. Their extensive topographical work left them but a very limited time for botanical research. Their few lichens were determined by Malme. The Danish "Danmark" expedition in 1906-08, under the command of Mylius Erichsen, devoted more time to lichens. Its botanist, Lundager, collected 68 lichens, identified by O. Galløe. The lichens were collected about Danmark Harbour, their headquarters ($76^{\circ} 25'$ N.). Lichenological research was an important botanical object for the two Norwegian expeditions in 1929 and 1930. We worked in the fjord district between the Liverpool coast in the south and Cape Wynn in the north, near the well known Sabine Island.

The determination of crustaceous lichens requires an immense amount of microscopical work. There are many of them in our

large collections, and we (*i. e.* Scholander and myself) have as yet only been able to work up a part of them. But the determination of our larger lichens has been published (Lyngé et Scholander: Lichens from North East Greenland, collected on the Norwegian Scientific Expeditions in 1929 and 1930. Oslo 1932).

We now have a fully representative collection of these lichens from North East Greenland. Its flora of "larger lichens," and also some genera of crustaceous lichens, is now so well known that it can be used as the basis for a comparison with the lichens of the same genera from other well explored Arctic regions. At the same time I have worked up the same genera in the almost inexhaustible treasures of undetermined Arctic lichens in the Oslo herbarium. I have also determined the same genera in Th. Fries's West Greenland collections, and I have revised the Copenhagen Greenland material of them. In this way I hoped to obtain really comparable material from large parts of the Arctic. For the small and often very inconspicuous lichens can only be extensively collected by trained lichenologists. Other botanists overlook them, even if they are excellent observers.

We now have good material of the larger lichens from the region between Ellesmere Land, west of Greenland (The Second Norwegian Arctic Expedition in the Fram, botanist: Simmons), across Greenland and Svalbard (the Spitsbergen region) to Franz Josef Land and Novaya Zemlya, and also from the Bering Strait district (the famous Vega expedition, botanist: Ernst Almquist, the lichens determined by Nylander and by Vainio).

Future expeditions will bring to light many additional facts on the lichen flora of these regions, also on the larger lichens. I may thus mention that in 1931 Scholander found *Physcia constipata* and fertile plants of *Dactylina ramulosa* in the North East Land of Svalbard. But, as it is, the available facts from these regions are supposed to be fully comparable.

Unfortunately our knowledge of the lichens of the Siberian coast west of the Bering Strait district is as yet insufficient. Several Swedish, Finnish and Russian expeditions have worked there. But much of the material still awaits determination, and other collections which have been determined are hardly large enough to be representative. In spite of important papers by Elenkin, Savicz, and others, I am of opinion that our knowledge of the lichen flora of this immense coast is still so incomplete that it would be misleading to use it for comparisons with the above mentioned regions.

Our knowledge of the lichens of the Canadian Arctic coast west of Ellesmere Land is so insignificant that we are obliged to pass over it in silence.

In 1929 all the East Greenland expeditions had to force their way through heavy pack-ice. Every day we risked having our ship destroyed. Should we succeed in getting through it? If so, how should we get back again to the sea and to our home? Such were our thoughts. We succeeded.

We were much astonished to find a land of almost constant sunshine. The penetrating Arctic gales, and all the fog, sleet and the icy cold rain, which we knew so well in Svalbard and in Novaya Zemlya, were entirely lacking during almost the whole summer. There was only one attack, and a serious one, towards the end of August.

The available data on the precipitation in North East Greenland are very incomplete. But we know that it is extremely low. Most probably there are many places in the desert of Sahara with a higher precipitation. The reason for this is supposed to be the high atmospheric pressure over the inland ice. The winds rush down the high, bold shores like the foehns of the Alps. From well known physical causes it becomes ever drier downwards. In the lowlands it is so dry that there is very little rain. The little precipitation they have comes during the winter as snow. There is hardly any rain during the time of vegetation. At the Norwegian meteorological station Myggbukta the annual precipitation is supposed to be about 300 mm.

Through the spring the moisture in the soil is sufficient. But during the month of July the ground dries up, the moisture evaporates, or it disappears in the ground. During August the ground becomes so dry that in the continental parts of the fjords we often saw salts that had been precipitated on the open surface of the soil. I have no remembrance of a day in Spitsbergen or in Novaya Zemlya when I returned from my excursion with dry feet. In Spitsbergen we often had to paddle for miles along the beach in order to find a spot that was dry enough for a tent camp. In North East Greenland there was no trouble whatever about such things.

The result of this dry climate is evident: a heath vegetation is developed. In July we find the beautiful flowers of *Cassiope tetragona* and *Arctostaphylos alpina* covering large areas, and *Empetrum nigrum* and *Betula nana* are common all over the land to the very shore

of the open sea. In the moist climate of Novaya Zemlya and Spitsbergen these plants are rare, in places lacking, plentiful only in some more continental parts, *e. g.* the inland end of Isfjorden (the Ice Fjord) in Spitsbergen.

It is not the object of the present paper to discuss the distribution of the Arctic Vascular plants. But I may perhaps be allowed another digression. According to Ostenfeld we know 181 species of Vascular plants from the Angmagsalik district, at 66° N. He records 169 different species from the mighty Scoresby Sound district, between 70°–72° N. Still farther north the two Norwegian expeditions in 1929 and 1930 obtained no less than 169 different species, exclusive of hybrids, in Eirik Raude's Land, between the Liverpool coast and Sabine Island, 73°–75° N.

These figures are not in every detail comparable. In the Norwegian records the genus *Draba* has been split up into narrower species than in the Danish records. But this difference is, on the whole, insignificant. The Vascular flora of the two southern regions has been quite as well explored as that of Eirik Raude's Land, by Kruuse and Hartz. Even with due allowance for the *Drabae* we find that the number of species is reduced by less than 10% from 66° N. to 73°–75° N., a distance that is about one-third of the distance between Angmagsalik and the North Pole.

This shows that the conditions of life must be very uniform on this enormous coast. Furthermore we know that several plants, as well as animals (the musk-ox, the polar wolf), must have immigrated to East Greenland by the northern route, north of Greenland. Few of them have reached the Angmagsalik district. They accordingly represent an extra contribution to the flora (and fauna) of the two northern districts, as compared with the flora (and fauna) of the Angmagsalik district. On the other hand the latter district has received elements that have not reached the northern regions, such as *Sedum acre* and others.

An Arctic traveller, who has had his experience in Spitsbergen and Novaya Zemlya, knows that the coast flora is poorer than is the flora of the more continental parts of the fjords. It will decrease again towards the inland end of the fjord if intensely glaciated. It is sufficient to compare the coast flora of Isfjorden (the Ice Fjord) in Spitsbergen with the rich flora of Sassen Valley and other continental valleys of the same fjord. We saw the same situation in Novaya

Zemlya. This is true for the Vascular plants and to some extent also for the lichens. But we must not forget that many lichens have an extreme need of nitrogen, and are, accordingly, restricted to the bird-cliffs of the coast. It is chiefly the southern lichens that retire from the coast. It might be suggested that the relatively rich flora of vascular plants in the northern districts in Greenland is due to the great areas of ice-free land along the immense fjords. Compared with them, the largest in the world, the fjords and the ice-free land of the Angmagsalik district are very small.

Arriving, with our former experience in the maritime eastern Arctic regions, we were much astonished to find a fairly rich flora along the coast in North East Greenland. Farther inland the flora varied in richness, on the friable chalky sandstones behind the diabases a rich flora, on the hard rocks a very poor one. At the inland end of the fjords it was decidedly poorer than on the coast, evidently due also to the dry, almost desert climate. It is, therefore, not probable that the great number of vascular plants in the northern fjords is due to the greater extent of the ice-free land.

In Novaya Zemlya these things are very different. We found 159 species of Vascular plants in Matotchkin Shar, a little more than 73° N., and only 70 species at Arkhangel Bay, just south of 76° N.

We must take into consideration the greater difference in the conditions of life between Matotchkin Shar and the intensely glaciated Arkhangel Bay district in Novaya Zemlya, as compared with Angmagsalik and Eirik Raude's Land in East Greenland. Yet I venture to suggest another factor, perhaps worthy of consideration: TIME.

In the region covered by our work in Novaya Zemlya there was not a single northern species that was lacking in the southern districts. Geologists and botanists agreed in regarding the northern parts of Novaya Zemlya as a land that had risen much and received its vegetation in relatively recent time, geologically speaking. We got the impression of a vegetation marching northwards.

We do not know much of the rapidity of the migration of Arctic Vascular plants. Failure to produce seeds does not check migration. In Novaya Zemlya I was much interested in that question. The summer was favourable, and generally I found ripe seeds as far north as I found the plants themselves. Plants that did not produce "diaspores" (*sensu* Sernander) locally were scarce and rare. The competition for the ground between related plants cannot be great.

In the real Arctic a continuous plant cover is very rare. Almost every seed has a fair chance of finding a place for germination. But I have seen very few seedling plants there. Apart from *Koenigia islandica*, which is supposed to be annual also in the Arctic, we find the viviparous grasses germinating, and some seedlings of the genera *Draba* and *Saxifraga*. Johannes Lid, the Norwegian expert on Arctic Vascular plants, has told me that he has seen seedlings of *Carex ursina* in Spitsbergen.

Are the Arctic seeds not capable of germinating or do the young seedlings meet so severe conditions of life at their start that they succumb? The case may be individually different for each species. From my own observation I might suggest the latter answer to be the more probable one. But this question requires exact experiments in Arctic biological stations, like so many other interesting questions on the biology of Arctic plants. We are much in need of such stations.

The rich development of runners of different kinds can only be of local importance for migration (grasses, *Carices*, *Saxifraga flagellaris* etc.). On the whole the propagation of the Arctic plants is supposed to be sufficient. But I find it probable that migration would be slow, as so many vital processes are in the Arctic. If that is so, the great number of species of Vascular plants in Eirik Raude's Land, North East Greenland, as compared with the Scoresby Sound district and Angmagsalik farther south, would suggest a considerable age for the North East Greenland flora.

We must not forget that there is a great difference between the number of species and the number of individuals. Though the number of species is almost identical over this enormous distance, it is sufficient to read Hartz's descriptions from Scoresby Sound, and Kruuse's from Angmagsalik, to see that the plant cover is much richer southwards.

The lichen vegetation is seriously influenced by the arid climate of North East Greenland. In the maritime Spitsbergen, and in Novaya Zemlya, the ground is full of brooklets and small and large rivers that drain the glaciers. Many lichens prefer these inundated places, especially *Pyrenocarpous* lichens. I have not yet determined our East Greenland aquatic *Pyrenocarpous* lichens, but the collection is very meagre. One of the few really common species is a *Staurothele* (*fusco-cuprea*?). Lichens that are characteristic of well drained fissures of vertical rocks, such as *Lecidea rubiformis*, develop mighty cushions on the naked soil, so dry is the soil in North East Greenland.

The most interesting lichen in North East Greenland is perhaps *Acarospora Schleicheri*, in Europe a Mediterranean species. Hartz found it in Scoresby Sound, and Scholander in King Oscar Fjord, a little farther north (1930). It is quite probable that the dry, warm summers make its existence possible. It is, perhaps, a relic from the Post Glacial warmer time.

In North East Greenland some lichen genera are represented by many species and by many common species, such as *Gyrophora*, *Peltigera*, *Solorina*, *Rinodina* etc. Other genera, e. g. *Parmelia*, *Rhizocarpon*, perhaps also *Lecidea*, concentrate in a few, very common, almost inevitable species. Their other species are few, and much less common than they usually are in the Arctic. Many instances of this have been mentioned in the paper by Scholander and myself.

Few crustaceous lichens were better represented in my Novaya Zemlya collection than the genus *Rhizocarpon*. I obtained 26 species, many of them common. In my North East Greenland collection I have only been able to find 8 species. Out of my several hundred *Rhizocarpon* plants about one-half belonged to one species, *Rhizocarpon disporum* (= *Rh. geminatum*); and *Rhizocarpon geographicum* was about two-thirds of the rest. The same is the case with several other genera.

This feature, that the vegetation concentrates in a few very dominant species, is well known from the heaths of Vascular plants. But I have formerly not been aware that the same would (or could) be the case with the lichens, also, in dry regions.

As far as I know we have no exact investigations on the content of the available plant nutriment in the ground in the Arctic. But on account of the cold, generally frozen soil the roots can only utilize the uppermost strata. And on account of the insignificant supply of decaying organic substance and the violent denudation by the streaming water there is but little fertile humus in the soil.

We can, therefore, understand the concentration of the Arctic vegetation in the bird-cliffs where sea-birds hatch in incredible numbers, and also on prominent rocks and stones where land-birds like to rest. It will be seen from my previous works on Arctic lichens that the lichens are still more dependent on the supply of manure than are the vascular plants. Very many of them are nitrophilous, and a lot of them coprophilous. In the bird-cliffs of Arkhangel Bay, just under 76° N., in Novaya Zemlya, I collected 208 species of lichens in 8 days.

And on Bear Island, where the sea-birds are so abundant, Th. M. Fries collected 185 species in 6 days (1868).

North East Greenland is one of the most inaccessible parts of the earth. In 1929 we had to force our way through a zone of unbroken polar pack-ice, almost 200 km. broad. The following year was a good ice-year, but 1931 was still worse than 1929. It is evident that the sea-birds cannot successfully start breeding on a coast where they are in danger of having ice of that kind just outside of their nests. Foraging will be impossible.

Danish scientists have told me that there is more open water near the outlet of Scoresby Sound. Here we find one bird-cliff on the Liverpool Coast, the northernmost in East Greenland. Farther north there are some land birds, and lichenologists will be glad to find the results of their droppings in the form of a rich lichen vegetation on prominent stones and rocks where they enjoy their siesta. There are also some scattered colonies of terns, who furiously attack every intruder. But the number of birds is equal to nothing as compared with the numbers in a bird-cliff, even if it is quite a small one.

The lack of nutriment from the bird manure and the arid climate are, in my opinion, the great restraining factors of the lichen flora in North East Greenland. We never found the coprophilous *Candelariella crenulata* there. In Spitsbergen and in Novaya Zemlya *Buellia coniops* is so plentiful that it colours the rocks along the beach. I have not yet seen it in my East Greenland collections. There are lots of other nitrophilous (coprophilous) lichens, common in other Arctic regions, but lacking in North East Greenland. Their number is so considerable that it much reduces the total number of lichen species in North East Greenland.

In the accompanying list (TABLE I) I have enumerated all the lichens at present known of some genera from North East Greenland, *i. e.* from Scoresby Sound and northwards. I have omitted some records, which I have been able to check and which I have found incorrect, and also a few which I have not been able to check, but which I have found too improbable (some southern species, even in Norway). In the first column of the enumeration I have recorded the greatest elevation above the sea, in meters, where the lichen in question was found by the Norwegian botanist P. F. Scholander during our expedition in 1930.

In Novaya Zemlya and in Spitsbergen I did not climb much in the

TABLE I. ON THE DISTRIBUTION OF SOME LICHENS OF NORTH EAST GREENLAND

	N. E. Greenland m.s.m.	Scandinavia	Spitsbergen	Nov. Zemlya	Bering Str.
1. MYCOCALICIUM SUBTILE (Ach.) Vain.		+	+		
2. SPHAEROPHORUS GLOBOSUS (Huds.) Vain.		+	+	+	+
3. FRAGILIS Pers.		+	+	+	+
4. DERMATOCARPON MINIATUM (L.) Mann.	900	+	+	+	
5. SPHAEROSPORUM Lynge	300	+			
6. CINEREUM (Pers.) Th. Fr.		+	+	+	+
7. DAEDALEUM (Krempfh.) Th. Fr.		+	+	+	
8. HEPATICUM (Ach.) Th. Fr.		+	+	+	+
9. ENDOCARPON PULVINATUM Th. Fr.		+	+	+	+
10. ARCTOMIA DELICATULA Th. Fr.		+	+	+	+
11. LEPTOGIUM PULVINATUM (Hoffm.) Cromb.		+	+	+	
12. LICHENOIDES (L.) Zahlbr.		+	+	+	
13. SATURNINUM (Dicks.) Nyl.		+	+	+	+
14. LECIOPHYSDIA FINMARKICUM Th. Fr.		+	+	+	
15. COLLEMA ARCTICUM Lynge		+	+	+	
16. PULPOSUM Ach.	700	+	+	+	
17. POLYCARPUM (Schaer.) Krempelh.	900	+	+	+	
18. RUPESTRE (Sw.) Rabh.		+	+	+	
19. SOLORINA BISPORA Nyl.	1350	+	+	+	
20. SACCATA (L.) Ach.	3-400	+	+	+	+
21. OCTOSPORA Arn.	900	+	+	+	
22. SPONGIOSA (Sm.) Anzi	350	+	+	+	+
23. CROCEA (L.) Ach.	900	+	+	+	+
24. NEPHROMA LAEVIGATUM Ach.		+	+		
25. PELTIGERA VARIOLOSA (Mass.) Gyeln.	580	+	+	+	+
26. VENOSA (L.) Hoffm.	300	+	+	+	+
27. SUOMENSIS Gyelnik	200	+	+		
28. RUFESCENS (Weiss) Humb.	1350	+	+	+	+
29. POLYDACTYLOIDES Nyl.		+			
30. POLYDACTYLA (Neck.) Hoffm.		+	+	+	+
31. MALACEA (Ach.) Fr.	400	+	+	+	+
32. ERUMPENS (Tayl.) Vain.	350	+	+	+	+
33. LEPTODERMA Nyl.	1200	+	+	+	
34. SCABROSA Th. Fr.		+	+	+	+
35. CLADONIA MITIS Sandst.		+	+	+	+
36. UNCIALIS (L.) Web.		+	+	+	+
37. COCCIFERA (L.) Willd.	1200	+	+	+	+
38. SQUAMOSA (Scop.) Hoffm.		+	+		
39. CENOTEIA (Ach.) Schaer.		+	+		
40. CARIOSIA (Ach.) Spreng.	1200	+	+	+	+
41. ACUMINATA (Ach.) Lynge	200	+	+	+	+
42. ELONGATA (Jacq.) Hoffm.	580	+	+	+	+
43. CORNUTA (L.) Schaer.		+	+		
44. LEPIDOTA Nyl.	300	+	+	+	+
45. CERVICORNIS (Ach.) Flot.		+	+	+	
46. FIMBRIATA (L.) Fr.		+	+		+
47. PYXIDATA (L.) Fr.	1350	+	+	+	+
48. CYANIPES (Somrft.) Vain.		+	+	+	
49. STEREOCAULON ALPINUM Laur.	1350	+	+	+	+
50. RIVULORUM H. Magn.	1200	+	+	+	

TABLE I. ON THE DISTRIBUTION OF SOME LICHENS OF NORTH EAST GREENLAND—(Continued)

	N. E. Greenland m.s.m.	Scandinavia	Spitsbergen	Nov. Zemlya	Bering Str.
51. STEREOCAULON FASTIGIATUM Anzi	900	+	+	+	+
52. DENUDATUM Flk.		+	+	+	+
53. GYROPHORA VIRGINIS (Schaer.) Frey	1350	+	+	+	+
54. DECUSSATA (Vill.) Zahlbr.	1350	+	+	+	+
55. POLARIS Scholander	1350	+	+	+	+
56. PROBOSCIDEA (L.) Ach.	1200	+	+	+	+
57. HYPERBOREA (Hoffm.) Ach.	360	+	+	+	+
58. ARCTICA Ach.		+	+	+	+
59. TORREFACTA (Lightf.) Cromb.	1350	+	+	+	+
60. EROSA (Web.) Ach.	1200	+	+	+	+
61. VELLEA (L.) Ach.		+	+	+	+
62. DEUSTA (L.) Ach.		+	+	+	+
63. CYLINDRICA (L.) Ach.	1600	+	+	+	+
64. PARMELIOPSIS AMBIGUA (Ach.) Nyl.		+	+	+	+
65. PARMELIA SUBOBSCURA Vain.	1600	+	+	+	+
66. INTESTINIFORMIS (Vill.) Ach.	450	+	+	+	+
67. PUBESCENS (L.) Vain.		+	+	+	+
68. MINUSCULA Nyl.	1600	+	+	+	+
69. STYGIA (L.) Ach.		+	+	+	+
70. ALPICOLA Th. Fr.		+	+	+	+
71. GROENLANDICA Lyngé.		+	+	+	+
72. SOREDIATA (Ach.) Th. Fr.		+	+	+	+
73. GRANULOSA Lyngé.	1350	+	+	+	+
74. INFUMATA Nyl.	1350	+	+	+	+
75. SAXATILIS (L.) Ach.		+	+	+	+
76. OMPHALODES (L.) Ach.		+	+	+	+
77. SULCATA Tayl.		+	+	+	+
78. CETRARIA HEPATIZON (Ach.) Vain.	900	+	+	+	+
79. NIVALIS (L.) Vain.	1350	+	+	+	+
80. CUCULLATA (Bell.) Ach.	400	+	+	+	+
81. ISLANDICA (L.) Ach.	360	+	+	+	+
82. CRISPA (Ach.) Nyl.	900	+	+	+	+
83. DELISEI (Bory) Th. Fr.	900	+	+	+	+
84. CORNICULARIA ACULEATA (Schreb.) Ach.	1350	+	+	+	+
85. RACEMOSA Lyngé.	360	+	+	+	+
86. DIVERGENS Ach.		+	+	+	+
87. EVERNIA MESOMORPHA Nyl.	220	+	+	+	+
88. DACTYLINA RAMULOSA Hook.		+	+	+	+
89. ALECTORIA OCHROLEUCA (Ehrh.) Nyl.	400	+	+	+	+
90. NIGRICANS (Ach.) Nyl.	580	+	+	+	+
91. JUBATA (L.) Ach.	1350	+	+	+	+
92. NITIDULA Th. Fr.		+	+	+	+
93. THAMNOLIA VERMICULARIS (Sw.) Ach.	1350	+	+	+	+
94. USNEA SULPHUREA (König) Th. Fr.	1350	+	+	+	+
95. XANTHORIA CANDELARIA (Ach.) Arn.	1350	+	+	+	+
96. PHYSCIA TRIBACIA (Ach.) Hedl.	1350	+	+	+	+
97. TENELLA Bitter	1350	+	+	+	+
98. MUSCIGENA (Ach.) Nyl.	1600	+	+	+	+
99. CONSTIPATA Nyl.	650	+	+	+	+
100. SCIASTRA (Ach.) Du Rietz.	900	+	+	+	+
101. CAESIA (Hoffm.) Nyl.	1350	+	+	+	+
102. INTERMEDIA Vain.		+	+	+	+

mountains. The work in the lowland was overwhelming, and the few ascents which I made did not induce me to do too much of it. The vegetation, including the lichens, rapidly diminished. It is possible, from what I saw in Greenland, that I underestimated the alpine lichen vegetation in the eastern Arctic. At least in one place, at Ullafjell in Bell Sound, Spitsbergen, I found a rich lichen vegetation up to 500 m.s.m. However that may be, I was immediately surprised to find a luxuriant lichen vegetation in North East Greenland up to altitudes where I should not have expected to find much in the other Arctic regions.

Unfortunately I was unable to follow up this observation myself. But the following year my friend, P. F. Scholander, joined the Norwegian East Greenland expedition. He was advised to give as much attention as possible to this problem, which he successfully did. His observations were supplemented by some by other members of the expedition. One short Arctic summer is certainly insufficient to clear up definitely a question of this kind, requiring equally much time and physical exertion. Most probably the altitudinal limit can be raised for many, perhaps for all, the species. But as it is, his results are really remarkable. About one-third of the lichen species which we have definitely determined (a little more than 90 species of these genera; we have no records for the other species) were found up to 1000 m.s.m. or more; 38 species were detected up to 900 m. or more; 23 species higher than 1350 m., and 3 species up to 1600 m.

If we exclude the southern species not found north of Scoresby Sound, I venture the suggestion that in Eirik Raude's Land, between the Liverpool Coast and Sabine Island, more than half the number of the lichen species of these genera ascend to 1000 m.s.m., or even higher. It is well known that lichens have a greater vertical range than Vascular plants. We do not know with certainty the percentage of Norwegian Vascular plants that are found at an altitude of 1000 m. or more in our country. Our botanists suggest something like 25%. In my book, *Studies on the Lichen Flora of Norway*, I have enumerated about 220 lichen species. About 100 of them ascend to this altitude.

We must, however, remember that this comparison is not quite just. Some of the 100 are alpine species that descend only to the forest line. Others are lowland species that ascend so high, recruited from the floras of the beach, the lowlands with their deciduous trees, and from the zone of Conifers. The same is the case with the Nor-

wegian Vascular plants. But in Greenland there is no zonation like this so far north. To make the comparison just, we should have to start from the timber line, in Southern Norway about 900–1000 m. above the sea level. Here the conditions of life are more comparable to those of the Greenland beach region. Unfortunately we do not know which of our Norwegian lichens ascend 1000 m. above the forest line. It is not supposed to be a great number. In Norway only the highest peaks attain that altitude. And we know that the conditions of life are very different on isolated peaks from what they are on great massives, such as we have in Greenland.

We will compare the lichen flora of Eirik Raude's Land, in North East Greenland, with the Norwegian alpine lichen flora. We find that out of these 102 lichens only 7 are lacking in Norway. The determination of the crustaceous lichens in our Greenland collections is not so far advanced that we can include them in this comparison. As far as I can see today it is hardly probable that the identity can be so great if we also include them.

One of the 7 species, *Peltigera polydactyloides*, will most probably be found in Norway, to judge from its general distribution. (I am not quite convinced that it really is a good, true species). Three of the other 6 have been described as new: *Dermatocarpon sphaerosporum*, *Parmelia groenlandica* and *Gyrophora polaris*. The distribution of the first two species is unknown.

Gyrophora polaris Scholander is common in this part of Greenland. I have also identified it in Th. M. Fries's collection from West Greenland, near Disko Island, and in Th. Wulff's collection from the northernmost part of Greenland; furthermore, from a few northern Spitsbergen localities and also from Franz Josef Land (it has generally been united with *Gyrophora proboscidea* in literature). But I have searched for it in vain in the Vega collection from Eastern Siberia, in my own Novaya Zemlya collection, and in the Danish collections from South Greenland and from Iceland. It is not found in the Norwegian mountains. It is a species of very northern and of western distribution in the Arctic. Should it not be found in the high American Rocky Mountains? It would be worth while to look after it there. If not, it is a strictly Arctic plant.

Usnea sulphurea is also a species of northern and western Arctic distribution. Simmons collected it in Ellesmere Land. It is common in the northern parts of Greenland, but there is no plant from South

Greenland in the Copenhagen herbarium. The Norwegian lichenologist, P. F. Scholander, an excellent observer, did not find it in South East Greenland, though he did his best to find it. It is so conspicuous that every botanist would have observed it. It is common in Jan Mayen, known from many places in Iceland (it was first described from Iceland), it is also common and widespread in Spitsbergen and in Franz Josef Land. But it is very rare in Novaya Zemlya, and it has never been collected east of Novaya Zemlya. It has never been collected on the European continent.

It is very interesting that *Usnea sulphurea* is also represented in the Antarctic by a very nearly related species. We have such plants in the Oslo herbarium, collected by Borchgrevink.

We cannot always maintain that all the Antarctic records of "*Usnea sulphurea*" or "*Usnea (Neuropogon) melaxantha*" refer to the same species, for several other species of the *Neuropogon* section are more common in the Antarctic, and they are not always distinguished from the so-called "*Usnea sulphurea*." This remarkable distribution will be discussed later in this paper.

Dactylina ramulosa is a circumpolar species of a remarkably northern distribution in the Arctic. It is also found in the American mountains and in the European Alps, but not in Scandinavia.

Parmelia subobscura, the last of the 7 species, is a circumpolar Arctic species. It much resembles an esorediated forma of the well known *Parmelia austerodes*, which is quite common in Scandinavia. I am not quite convinced that it really is a proper species, distinct from *Parmelia austerodes*, for in the Arctic soredia are generally poorly developed, and it would be quite natural to regard *Parmelia subobscura* as an Arctic esorediated forma of *Parmelia austerodes*.

On the whole we find only a few North East Greenland species of these genera that are lacking in Norway. The resemblance is so great that it approaches identity. If we found in all 102 species of certain lichen genera on a Norwegian mountain it would be quite probable that 7 of them would be lacking on the neighbouring mountain.

Professor Warming of Copenhagen maintained that the Denmark Strait between Greenland and Iceland was a line of distinction between a western American flora in Greenland and an eastern European flora, represented by its western outposts in Iceland. Professor Nathorst of Stockholm was of opinion that the line of distinction

should be the inland ice of Greenland. The flora of East Greenland is largely European, with some American immigrants, according to him. My results are strongly in favour of Nathorst's view, as far as the lichens are concerned. We should, however, remember that only a part of our lichen collections have as yet been determined. It is possible that the determination of the crustaceous lichens will modify this opinion. But I have already determined so many of them that an eventual modification seems improbable; anyhow it cannot be great.

It is of much interest to know whether a conformity between the flora of North East Greenland and the flora of Norway can be proved for other plants also. A young Norwegian botanist, Mr. Reidar Jørgensen, has studied the Vascular plants of the highest mountains in Southern Norway, called Jotunheimen. His studies necessitated physical strain equally much as botanical knowledge. In TABLE II we find all the species of Vascular plants which he detected higher than 2000 meters above sea-level in these mountains. The first column records his highest find of the plant in question (in meters) in Jotunheimen, the second the number of finds down to the timber line which is here about 900–1000 meters above sea-level, expressing the frequency of the plant in the Jotunheimen, the third column the presence or absence (—) respectively in North East Greenland (Gr.), in the Svalbard region (Sv.), and in Novaya Zemlya (N. Z.). The data on their Arctic distribution have been supplied by the present author. It is evident from the enumerations that nearly all the plants which are found in the really high Norwegian mountains have a wide distribution in the Arctic.

If we could leave the history of the plants quite out of consideration, it would be a simple and reasonable explanation that we have here a number of plants that are exceptionally well adapted to the severe conditions of life in the Arctic and on the highest mountains in Norway. But, if we will also include their history in our considerations, we shall have to discuss two other possibilities. Did the ice-cover sweep away all plants from the Arctic and from the Scandinavian peninsula, or did it leave some refuges, nunataks or ice-free coasts of varying size where such hardy mountain plants could have persisted?

If preference must be given to the former view it is very hard to explain why just the same selected number of plants should have made the same long migrations. The fundamental question can only be

TABLE II. VASCULAR PLANTS ATTAINING 2000 METERS ABOVE SEA-LEVEL IN JOTUNHEIMEN, NORWAY

	Highest find, meters	Number of finds in Jotunheimen	Greenland	Svalbard	Novaya Zemlya
RANUNCULUS GLACIALIS	2300	264	Gr.	Sv.	N. Z.
POA LAXA	2300	215	—	—	—
FESTUCA VIVIPARA	2300	137	Gr.	Sv.	N. Z.
SAXIFRAGA OPPOSITIFOLIA	2300	42	Gr.	Sv.	N. Z.
DRABA FLADNIZENSIS	2300	25	Gr.	—	N. Z.
SEDUM ROSEUM	2200	154	Gr.	Sv.	N. Z.
SAXIFRAGA GROENLANDICA	2200	68	Gr.	Sv.	N. Z.
TRisetum SPICATUM	2200	154	Gr.	Sv.	N. Z.
CERASTIUM ALPINUM	2200	132	Gr.	Sv.	N. Z.
ANTENNARIA ALPINA	2200	120	Gr.	—	—
LUZULA SPICATA	2200	103	Gr.	—	—
POLYGONUM VIVIPARUM	2200	127	Gr.	Sv.	N. Z.
SAXIFRAGA CERNUA	2200	41	Gr.	Sv.	N. Z.
LUZULA CONFUSA	2100	185	Gr.	Sv.	N. Z.
SALIX HERBACEA	2100	254	Gr.	Sv.	—
SILENE ACAULIS	2100	141	Gr.	Sv.	N. Z.
OXYRIA DIGYNA	2100	111	Gr.	Sv.	N. Z.
SAXIFRAGA RIVULARIS	2100	32	Gr.	Sv.	N. Z.
POA ALPINA VIVIPARA	2100	10	Gr.	Sv.	N. Z.
SIBBALDIA PROCUMBENS	2100	115	Gr.	Sv.	N. Z.
ERIGERON UNIFLORUS	2100	139	Gr.	Sv.	N. Z.
MINUARTIA BIFLORA	2100	33	Gr.	Sv.	N. Z.
SAXIFRAGA NIVALIS	2100	28	Gr.	Sv.	N. Z.
SAUSSUREA ALPINA	2100	131	—	—	—
POTENTILLA ALPESTRIS	2100	82	—	—	—
RANUNCULUS PYGMAEUS	2100	46	Gr.	Sv.	N. Z.
CAREX RUPESTRIS	2100	17	Gr.	Sv.	N. Z.
TARAXACUM CORNUTUM	2100	6	—	—	—
CARDAMINE BELLIDIFOLIA	2000	87	Gr.	Sv.	N. Z.
DESCHAMPSIA ALPINA	2000	63	Gr.	Sv.	N. Z.
CERASTIUM TRIGYNUM	2000	31	Jan Mayen	—	N. Z.
TARAXACUM CROCEUM	2000	45	—	—	—
GNAPHALIUM SUPINUM	2000	37	South Greenl.	—	—
POA ALPINA	2000	27	Gr.	Sv.	N. Z.
ANTENNARIA DIOICA	2000	18	—	—	—
TARAXACUM COCHLEATUM	2000	7	—	—	—

solved by the geologists. We botanists can only say that our botanical evidence is in favour of the persistence theory. We can understand short migrations, but if the migrations had been really long, over the Oceans and over vast continents, how should we explain the uniformity of the floras of such distant regions?

It can be objected that the comparison is not quite just. We ought to have compared the whole North East Greenland flora with the

entire Norwegian alpine flora, growing higher than the timber line. There is a considerable number of plants in North East Greenland, not found in our mountains, perhaps American immigrants. On the other hand there are many plants in our mountains, which are lacking in North East Greenland. But such entire "floras" of vast regions are so heterogeneous things that statistical comparisons must necessarily be very problematical. There are several degrees of a lie, said the Danish botanist, W. Johannsen, the highest of which is biological statistics! However that may be, the plants from our highest mountains of Norway include just the plants which we must consider adapted to live in ice-free refuges during the different glaciations, and it is a very remarkable fact that these floras are so uniform over large areas.

The difference between the lichen flora of North East Greenland and that of Svalbard (Spitsbergen and the adjacent islands) is considerably greater: 20 of these Greenland lichens are lacking in Svalbard, though it is possible that some of them will be found there. Scholander found *Physcia constipata* in Svalbard in 1931; it had been collected in Greenland, in 1930, also by Scholander, an addition to the Arctic lichen flora. But the lichen flora is now much better explored in Svalbard than in Greenland.

Let us discuss the 20 Greenland lichens which are unknown from Svalbard. Firstly, two of the three new Greenland species are lacking in Svalbard. One of them, *Gyrophora polaris*, is found there.

Five of the 20 are southern species in East Greenland, recorded as far north as Scoresby Sound, but not farther north, in Eirik Raude's Land. It is not unreasonable to regard them as pilgrims that have wandered northwards from the fjords of the present Julianehåb district in Southern Greenland, the old Eystribygd, where the ancient colonists from Iceland and Norway held their position during many centuries, before they succumbed. It is the "Riviera" of Greenland. If so, we should perhaps have to regard them also as relic plants from a warmer postglacial time. Svalbard is not connected with a southern region of a clement climate, from which a southern flora could have been recruited, and the present summer climate in Svalbard is not clement.

There is only one of the 20 species which is fairly common in North East Greenland, viz. *Peltigera Suomensis*, nearly related to *P. rufescens*, if not identical. I have repeatedly found this species in Nor-

way; it has been named *Peltigera spuria* in our literature. In Lapland it has a distinct predilection for the old fire-places of abandoned Lapponian camps. In Greenland I often found it in old Esquimaux residences, but it is not restricted to them. In Spitsbergen it should be looked after at the old Dutch settlements on Amsterdam Island; it would really be a satisfaction to find it there.

As far as I can see all the other 19 species are more or less rare in North East Greenland. Though we paid special attention to the rare species, and collected them extensively, we have more material of almost any one of the common species alone in our Greenland collections than we succeeded in finding of these 19 species combined.

There is, accordingly, a considerable difference in the species lists from the North East Greenland and the Svalbard region. But the common species are the same. And they are much more important for geographical considerations than isolated finds of rare species. If we are to find out the character of the Norwegian flora, we shall have to give more attention to *Pinus silvestris* and to *Picea Abies* (= *P. excelsa*) than to the rarest plants, even if the latter are so numerous that they count for much more in a simple enumeration. If a scientist, who was not a trained lichenologist, collected lichens in North East Greenland and in Svalbard, he would perhaps return with something like 60 species from either region, as such people generally do. If he did not work in the bird-cliffs of Spitsbergen, he would bring home almost the same lichens from either region.

We further find that 20 of these North East Greenland lichens are lacking in Novaya Zemlya. And we find that out of these 20 13 are also lacking in the Svalbard region. The greater part of these species are southern plants. We should not be astonished to find them so far north in East Greenland, on account of its clement summers that must be more favourable to them than the maritime cold and moist summers of the Eastern regions. It is quite natural that such species should be lacking in the Svalbard (Spitsbergen) region, also on account of its great isolation from southern regions; the distance from Spitsbergen to North Cape in Norway is a long one.

Out of the 20 species two only are common in North East Greenland: *Peltigera Suomensis* and *Gyrophora polaris*. We have just discussed the former species. The latter is a species of western and northern distribution, found as far east as Franz Josef Land. All the other 18 are "rari nantes" in North East Greenland. With the

exception of the two species just mentioned all the other common North East Greenland lichens of these genera are also found in Novaya Zemlya—each and every one of them.

We must go far east to find the next region where the lichen flora is so well explored that we can draw comparisons: to the Bering Strait region, 150° west of East Greenland, just on the other side of the polar basin. After an exceptionally favourable voyage the famous "Vega" froze in at Pitlekai, near the Strait, on the 28th of September, 1878. It was imprisoned until July 18th, 1879, when the ice broke up. It was a bitter disappointment to the members of the expedition to lose one year, but a mighty stroke of luck to botany, for their botanist, Dr. E. Almquist, brought home large collections of lichens from the winter quarters.

There are about 60 species in common in his collections from the Bering Strait region and in our East Greenland collections of the genera treated in the present paper. We cannot state the number with absolute certainty without an examination of some critical species in the "Vega" collections. Out of the about 40 North East Greenland species that are lacking in the Bering Strait region, several species are common in East Greenland. We will especially mention the interesting species *Usnea sulphurea* and *Gyrophora polaris*, which have a western Arctic distribution. But there are also other common species amongst them.

On the other hand, the Bering Strait region (we here only consider the Strait itself and the adjacent part of the Siberian coast) contains eastern species that are lacking in East Greenland. The Strait must have been a gateway for plant immigration of the highest importance for, to judge from the lichens of the "Vega" expedition, these regions must be among the richest in the Arctic, botanically speaking. The "Vega" expedition found about 400 different species of lichens, about the same number as the Norwegian Novaya Zemlya expedition brought home.

It is only to be expected that the lichen flora of this remote region should be so different from that of North East Greenland. But in reality the difference is not so great as the figures suggest, for the vegetation is much more similar than are the lists of the flora. Let us first remember that the "Vega" expedition dates 50 years back. Since then science has advanced. Several new species have been described, and it is highly probable that a modern lichenologist

would find some of them on the Arctic coast near the Bering Strait, as we have done in the western Arctic.

Out of the 60 species common to both regions only 10 species are rare in North East Greenland. They are chiefly southern species. This again brings before us the well established fact that North East Greenland is an exceptionally favourable country for southern species, in spite of its high latitude.

We find, accordingly, that about 50 of the common North East Greenland lichens out of these genera are also found near the Bering Strait. That is by far the greater part of the common species in our Greenland region. It is just one-half of the whole North East Greenland flora of these genera. And they more than counterbalance the other half with respect to frequency and importance in the Greenland vegetation. It can safely be said that if a non-lichenologist collected lichens in these regions, he would bring home a (small) collection from either region, consisting of almost the same species. Our result is that a very large percentage of the lichens (of these genera) that are common in North East Greenland have a wide Arctic distribution; the greater part of them are circumpolar.

I will define as circumpolar a lichen that is found in Greenland (inclusive of Ellesmere Land), the Svalbard region, Novaya Zemlya and the Bering Strait region, north of the Strait. As long as the Siberian and the Canadian Arctic coasts are so insufficiently explored, we cannot, unfortunately, include the few scattered records from these immense ranges in our discussions. Out of the well over 100 species, which I have here considered, I now regard almost 50 as circumpolar. Undoubtedly further research will increase the number. And the circumpolar lichens are obviously those that are common in all the regions, or in several of them.

Can we connect their frequency and their great distribution with special manners of dispersal, which we could suppose to be peculiarly effective?

In Arctic lichens we find three possible manners of dispersal, *viz.* by means of spores, soredia and thallus fragments. The soredia are certainly not important. They are found only in a few Arctic lichens, and, if found, they are often poorly developed, corticated and certainly inefficient. But we must confess that the circumpolar sorediated lichens are common where I have seen them, with the exception of the two *Cladoniae*. All the non-circumpolar sorediated lichens are rare.

We can safely say that apothecia are either entirely lacking or very rare in each of the sorediated lichens. If their soredia really are so ineffective as I suppose them to be, they are chiefly propagated by thallus fragments, and they should then be added to the second column in the following enumeration (TABLES III AND IV).

TABLE III. CIRCUMPOLAR LICHENS OF NORTH EAST GREENLAND

Apothecia well developed	Apothecia lacking or very rare	Soredia developed (effective?)
DERMATOCARPON CINEREUM HEPATICUM	SPHAEROPHORUS GLOBOSUS	PELTIGERA ERUMPENS CLADONIA COCCIFERA f. PYXIDATA f.
ARCTOMIA DELICATULA	PELTIGERA RUFESCENS, POLYDACTYLA, MALACEA and SCABROSA	PARMELIA SOREDIATA GRANULOSA SULCATA
SOLORINA SACCATA more probably S. BISPORA	CLADONIA MITIS, UNCIALIS, COCCIFERA, CARIOSA, ELONGATA, LEPIDOTA and PYXIDATA	XANTHORIA CANDELARIA PHYSICIA TRIBACIA CAESIA
SOLORINA SPONGIOSA CROCEA	STEREOCAULON ALPINUM and DENUDATUM	
GYROPHORA PROBOSCIDEA HYPERBOREA ARCTICA TORREFACTA EROSA	PARMELIA PUBESCENS, MINUSCULA, ALPICOLA, SOREDIATA, GRANULOSA, SAXATILIS and OMPHALODES	
PARMELIA PUBESCENS ALPICOLA SAXATILIS	CETRARIA HEPATIZON, NIVALIS, CUCULLATA, CRISPA, ISLANDICA and DELISEI	
CETRARIA HEPATIZON	CORNICULARIA ACULEATA ALECTORIA OCHROLEUCA and NIGRICANS THAMNOLIA VERMICULARIS PHYSICIA MUSCIGENA and SCIASTRA	

In these columns we find almost the same proportion for the widespread circumpolar Arctic lichens as for the less widespread or local species. We cannot conclude that any one of these manners of multiplication is more effective for migration than another. We must find other causes. The number of species is not so great that a comparison between the percentages would be of interest. And even if it were larger, statistical considerations should be used with great care in biology. They easily conceal causalities.

Let us compare those species, which are always, or nearly always, sterile in the Arctic, with the same species, when growing under more

TABLE IV. NON-CIRCUMPOLAR LICHENS OF NORTH EAST GREENLAND

Apothecia well developed	Apothecia lacking or very rare	Soredia developed (effective?)
MYCOCALICIUM SUBTILE DERMATOCARPON MINIATUM SPHAERO- SPORUM DAEDALEUM	SPHAEROPHORUS FRAGILIS LEPTOGIUM PULVINATUM COLLEMA PULPOSUM PELTIGERA VARIOLOSA and POLYDACTYLOIDES	PELTIGERA LEPTODERMA CORNICULARIA RACEMOSA EVERNIA MESOMORPHA PHYSICIA TENELLA
LECIOPHYSMA FINMARKICUM ENDOCARPON PULVINATUM COLLEMA ARCTICUM POLYCARPUM PELTIGERA VENOSA SUOMENSIS STEREOCAULON RIVULORUM (often sterile) STEREOCAULON FASTIGIATUM (often sterile) GYROPHORA VIRGINIS POLARIS CYLINDRICA	CLADONIA SQUAMOSA, CENOTEA, ACUMINATA, CORNUTA, LEPIDOTA, CERVICORNIS, FIMBRATA, PYXIDATA and CYANIPES GYROPHORA DECUSSATA, VELLEA and DEUSTA PARMELIA SUBOBSCURA, INTESTINIFORMIS, STYGIA, GROENLANDICA and INFUMATA ALECTORIA JUBATA USNEA SULPHUREA PHYSICIA CONSTIPATA and INTERMEDIA	

favourable conditions in southern regions. We find that the greater number are sterile under all conditions of life. They are genotypically sterile. But there are also some species, which we could not have placed in that category if we had been examining the lichen flora of a southern country, *e. g.* *Peltigera polydactyla*, *P. malacea* and *P. variolosa*, several *Cladoniae*, and *Parmelia stygia*.

We can safely conclude that in some lichens the Arctic conditions of life make the formation of apothecia difficult, if not impossible. If such lichens had no other means of propagation they would be quickly eliminated from the Arctic flora. As it is, they are quite as common and as widespread as most other lichens.

If the different distribution of these lichens cannot be explained by their different manner of dispersal, we might suggest that it could be due to their different rapidity of growth. That is possible. But lack of well established knowledge on that point prevents us from giving much attention to that possibility.

I do not, however, think it an important factor. We know that the rapidity of growth is very different in different lichens. Some *Cladoniae* have a very slow growth. In the Arctic a *Cladonia alpestris*

would certainly require 50 years or more to become full-grown. Related *Cladoniae*, such as *C. rangiferina* and *C. silvatica* (in the Arctic *C. mitis*) have a considerably quicker growth. And that is still more the case with other *Cladoniae*, such as *C. coccifera* and the other red-fruited species.

The non-circumpolar *Peltigerae* cannot be supposed to have a slow growth. The same must be the case with the *Stereocaulons*, which we know to be quick growers. I cannot believe that the 3 non-circumpolar *Gyrophorae* could be slow growers; a species such as *Gyrophora deusta* should, on the contrary, be a quick grower.

Let us not forget the geographical factors. The distances between the continents are not so great in the Arctic as they are farther south. The distance between Norway and East Greenland is only one third of the distance between Norway and New York. The distance between East Greenland and Spitsbergen is much shorter still. The distance from the North East Land of Svalbard and Franz Josef Land is next to nothing, and from the latter archipelago to Novaya Zemlya it is also so short that many plant diaspores (*sensu* Sernander) must have been able to pass. Along the Siberian and the Canadian coasts there is a continuous way overland.

The oversea distances have formerly been still shorter than they are today. During the greatest glaciation much water was frozen up in the enormous glaciers, and the sea-level was lower than today. One of our leading geologists has suggested to me that it could have been about 200 meters lower than it now is. That would have exposed much land, which is now under the sea.

If we could venture a consideration of the Wegener hypothesis the great conformity of the lichen vegetation would be easily explained, on the supposition that the lichens were old enough, geologically speaking. Many facts are in favour of this fascinating hypothesis, others are against it. As long as it is so hypothetical, we should perhaps not use it too much as a platform for constructions.

The same is the case with the supposed land-bridge between Greenland and Europe over Iceland and the Faeroes, which played an important part in the considerations of Nathorst. But can this narrow bridge really explain so general things as the uniformity of distant Arctic floras?

There is but one genus of Crustaceous lichens, the distribution of which is so well known throughout the Arctic that we can use it for

general discussions, *viz.* the genus *Rhizocarpon* (TABLE V). We are indebted to Dr. E. Almquist, the Vega Expedition, for our material from the Bering Strait, determined by Nylander and Vainio. The data on *Rhizocarpons* from Novaya Zemlya and from Spitsbergen are based on my own determinations; the plants are found in the Oslo Botanical museum. I have also revised the material of this genus from Greenland, found in the leading Scandinavian herbaria.

Unfortunately, I have not seen the material from the Bering Strait region; it is possible that some of Nylander's new species will prove to be identical with other *Rhizocarpons*, recorded from the other regions. Apart from these eastern plants I am responsible for all the determinations. They may be correct or not, but the same name stands for the same species throughout. We have the great advantage that the determinations are fully comparable.

These lists tell a story very different from that of the larger lichens, the Foliaceous and Fruticulose lichens. We find a very small number of circumpolar *Rhizocarpons*, only 6 species out of 48 acknowledged Arctic species. Some species have only been recorded from the Atlantic sector, others have their distribution in the eastern sectors. Out of the 48 species, 4 are (so far) only known from Greenland, 8 are restricted to Novaya Zemlya, and no less than 16 to the Bering Strait region.

There is every reason to believe that a more intense exploration by competent lichenologists will to some extent bridge over such large regional differences. But I am fully convinced that these regions are so well explored, lichenologically, that there must be real, and large, regional differences. First, we find that the genus is much better represented in the eastern than in the western Arctic. The result from the Bering Strait region was obtained by one single expedition which collected 29 *Rhizocarpons*. The same is the case with Novaya Zemlya where the number is 27 *Rhizocarpons*. After about a century of exploration we have only 17 species of *Rhizocarpon* from immense Greenland and only 14 from Spitsbergen.

Greenland is a large continent, rather than an island, covering 23 degrees of latitude, and with more than 1/7 of its area ice-free. Yet its entire known lichen flora is poorer in number of species than is the inconsiderable area along the west coast of Novaya Zemlya, 4 degrees of latitude, and the very small area of Bering Strait with its nearest surroundings westwards. It is not so remarkable that the

TABLE V. ARCTIC RHIZOCARPONS

	Greenland	Svalbard	Nov. Zemlya	Bering Str.
CIRCUMPOLAR SPECIES.				
1 (1). RHIZ. COPELANDII (Kbr.) Th. Fr.	+	+	+	+
2 (2). DISPORUM (Naeg.) Müll. Arg.	+	+	+	+
3 (3). GEOGRAPHICUM (L.) DC.	+	+	+	+
4 (4). GRANDE (Flk.) Arn.	+	+	+	+
5 (5). HOCHSTETTERI (Kbr.) Vain.	+	+	+	+
6 (6). POLYCARPUM (Hepp) Th. Fr.	+	+	+	+
WESTERN ARCTIC SPECIES (Greenland).				
7 (1). RHIZ. CRYSTALLIGENUM Lyngé	+			
8 (2). GROENLANDICUM Lyngé	+			
9 (3). OCCIDENTALE Lyngé	+			
10 (4). VIRIDIATRUM (Flk.) Kbr.	+			
ARCTO-ATLANTIC SPECIES (Greenland-Svalbard-Novaya Zemlya).				
11 (1). RHIZ. BADIOATRUM (Flk.) Th. Fr.	+	+	+	
12 (2). CHIONOPHILUM Th. Fr.	+	+	+	
13 (3). DISTINCTUM Th. Fr.	+		+	
14 (4). JEMTLANDICUM Malme	+	+	+	
15 (5). OBSCURATUM (Ach.) Mass.	+	+	+	
16 (6). RITTOKENSE (Hellb.) Th. Fr.	+	+	+	
17 (7). PSEUDOSPEIREUM (Th. Fr.) Lyngé		+	+	
NOVAYA ZEMLYA SPECIES.				
18 (1). RHIZ. ALBIDUM Lyngé			+	
19 (2). ALPICOLA (Hepp) Flagey			+	
20 (3). ANSERIS Lyngé			+	
21 (4). ATROFLAVESCENS Lyngé			+	
22 (5). CINEREOFLLAVESCENS Lyngé			+	
23 (6). CINEREONIGRUM Vain.			+	
24 (7). PETRAEUM (Wulf.) Mass.			+	
25 (8). VERRUCOSUM Lyngé			+	
EASTERN ARCTIC SPECIES (Svalbard-Novaya Zemlya-Bering Strait).				
26 (1). RHIZ. CHIONEUM (Norm.) Th. Fr.		+	+	+
27 (2). EXPALLESCENS Th. Fr.		+	+	+
SIBERIAN ARCTIC SPECIES (Novaya Zemlya-Bering Strait).				
28 (1). RHIZ. CHIONOPHILOIDES (Vain.) Lettau			+	+
29 (2). LAVATUM (Fr.) Arn.			+	+
30 (3). PHALEROSPORUM Vain.			+	+
31 (4). RORIDULUM Th. Fr.			+	+
ARCTO-PACIFIC SPECIES (Bering Strait).				
32 (1). RHIZ. ALBOPUNCTATUM (Vain.) A. Zahlbr.				+
33 (2). "ATROALBUM" Flot. (?)				+
34 (3). ATROALBENS (Nyl.) A. Zahlbr.				+

TABLE V. ARCTIC RHIZOCARPONS—(Continued)

	Greenland	Svalbard	Nov. Zemlya	Bering Str.
ARCTO-PACIFIC SPECIES (Bering Strait).				
35 (4). RHIZ. ATROCAESIUM (Nyl.) ¹				+
36 (5). DECINERASCENS (Nyl.) A. Zahlbr.				++
37 (6). DETINENS (Nyl.) A. Zahlbr.				++
38 (7). "EUPETRAEOIDES (Nyl.)" (?)				++
39 (8). "EXCENTRICUM (Ach.)" (?)				++
40 (9). INFERNULUM (Nyl.)				++
41 (10). LEUCOPSEPHUM (Nyl.) A. Zahlbr.				++
42 (11). MELANEIMUM (Vain.) A. Zahlbr.				++
43 (12). OCHRODELUM (Nyl.) A. Zahlbr.				++
44 (13). POSTUMUM (Nyl.) Th. Fr.				++
45 (14). PRAEBADIUM (Nyl.) A. Zahlbr.				++
46 (15). SEMOTULUM (Nyl.) A. Zahlbr.				++
47 (16). SUBALPICOLUM (Nyl.) A. Zahlbr.				+
AMERICAN ARCTIC SPECIES (Bering Strait-Greenland).				
48 (1). RHIZ. SUPERFICIALE (Schaer.) Malme	+			+

lichen flora of the isolated Svalbard islands, the most important part of which is the island Spitsbergen, should be so poor in number of species; we have here an attenuated Scandinavian alpine flora with an addition of some specially Arctic lichens, and very few peculiar, perhaps endemic, species.

The difference might be due to historical causes. During the great Glacial epochs glaciation was much more intense in the western Arctic than in the East; as far as I know the Bering Strait region was not glaciated at all. Novaya Zemlya was certainly intensely glaciated. We do not know whether there were small ice-free refuges, or not. The botanical evidence is in favour of the former view, but the question can only be solved by the geologists. But however that may be, Novaya Zemlya was in easy connection with unglaciated areas through the Ural mountains and their slopes and the adjacent lowlands.

¹ The four lichens, *Rhizocarpon atrocaesium*, *infernulum*, *eupetroides* and *excentricum*, were referred to the genus *Lecidia* by Nylander who did not admit *Rhizocarpon* as a valid genus. It is much to be desired that these highly critical lichens should be studied in detail by a competent modern lichenologist. The author has not had the opportunity to do it; therefore he is unable to give definite combinations of the names, and he has found himself obliged to use the above preliminary combinations, "*Lecidia parapetraea atrocaesia*" or "*Lecidia atrocaesia*" was described by Nylander in *Flora*, 1885, p. 446; "*Lecidia infernula*" in *Flora*, 1885, p. 440; "*Lecidia eupetroides*" in *Flora*, 1875, p. 12; "*Lecidia excentrica*" was mentioned by Nylander in *Enum. Lich. Freti Berh.*, 1888, p. 234.

Biologically Greenland is isolated. Only along its highly Arctic north-west coast is there a narrow strait, separating it from Ellesmereland. But Ellesmereland is certainly no fertile Goshen. Farther south there are broad seas on all sides, separating Greenland from Labrador and Arctic Canada in the west; on the east there is the whole Atlantic Ocean.

If any group of plants should be able to show a persistence from (or through) Glacial epochs, it certainly must be the lichens. In Novaya Zemlya I detected more than 200 different species of lichens, during 5 days of work, and only 70 different species of Vascular plants, on a very narrow strip of land just south of 76° N. between the glaciated land and the sea. And we know about 200 different species of lichens from the Antarctic continent and the nearest islands, in spite of an exceptionally intense glaciation.

If this view is correct, Vascular plants must have an easier migration than lichens, in spite of their heavier diaspores (*diaspore* is a term, introduced by Sernander, for any part of a plant by which it is propagated, a seed, a spore, a thallus-fragment, a soredium, and the like). The idea is not unreasonable. A seed is a wandering pantry, a spore or a thallus-fragment a poor beggar, immediately dependent on the food conditions of its place of germination, certainly no inviting position in the Arctic. I may add that Professor Carl Christensen, the well known Danish expert on ferns, once told me that there are very many tropical ferns with a very limited range of distribution, suggesting difficult migration, in spite of the easy dispersal of their small spores.

We have found that parts of the Arctic flora are very uniform all over this immense area. The reason for this is a problem of such a generality that it demands an explanation of equally general character. *I can only explain this great conformity of the lichen flora in so distant regions on the supposition that many of the species are very old in their present area, or in adjacent areas.*

Backwards our thought will naturally stop at the time of the great ice ages. We do not know the number of years that have rolled on since the days of the last great glaciation. Being a botanist myself and not a geologist I do not venture to write much on this intricate question. But my geological friends have told me that we have approximate ideas. According to the results of De Geer and his followers something like 40,000 years represent a probable time.

We know that during the greatest glaciation immense areas were covered with mighty glaciers, resembling those of the present Antarctic continent. These areas were inaccessible to any vegetation. Since then a new vegetation has followed the retiring ice. In the present Arctic we find a vegetation of hardy plants, not covering the ground and not so great in number as farther south, but yet much more considerable than the average person supposes. Even trained botanists must be surprised to see it.

Is it possible that so many lichens could have attained their present circumpolar distribution during the time that has elapsed since the days of the great glaciation?

Of course these plants are wonderfully adapted to their present conditions of life; just go and see them. Otherwise they would not have been there. But we know the extreme slowness of all vital processes in the Arctic. Growth in general is incredibly slow there. A bud requires years to mature, and the result is a short shoot with a few leaves, or a flower. We must expect the same slow growth for the Arctic lichens, although we are obliged to confess that our exact knowledge on this interesting point is next to nothing.

It is impossible to deny that many Arctic lichens can have migrated and spread extensively since the ice age. But on the other hand it is quite evident, from their present distribution, that many Arctic plants must be old plants on the earth. The circumpolar *Alectoria nigricans* reaches right down to the mountains of New Zealand where Du Rietz found it to be common. The West-Arctic *Usnea sulphurea* is found, almost identically, in Antarctic regions also. The distribution of the two species of *Dactylina* will be discussed at the end of the present paper. Plants such as these must be old. They could not have attained their present distribution in recent times. Remember the wide distances, the great Oceans, which their diaspores must have covered, the mountains and the deserts which they must have crossed.

I may mention that these few species, which were chosen for examples, have rather large diaspores. They have no soredia. Apothecia are either entirely lacking, or they are so rare that it is a great sensation to find them. So they have only thallus-fragments left for their diaspores.

It would have been much easier to discuss the distribution of Arctic lichens if our knowledge of the alpine and nivale lichens had not been so sorely deficient outside of Europe. There is hardly an interesting

spot on the earth not visited by well equipped American expeditions. But what do we know of the lichens of the high Rocky Mountains? Our knowledge has not increased much since the days of Tuckerman. I am convinced that we should find a lot of Arctic lichens there. The best place to start the research work would perhaps be somewhere near the limit of the greatest glaciation. The same is the case with the Ural and the Altai, which must necessarily be quite as important as the Rockies.

The habitats of some lichens in our own Norwegian mountains also suggest a great age. We have a considerable number of lichens that are either confined to places that have most probably been nunataks during the ice age, or that largely prefer such places. I may mention *Gyrophora rigida*, *G. fuliginosa*, *G. vellea* and *Acarospora chlorophana*. If this view is correct, we have here an interesting case of the persistence of plants.

If we call these places "probable nunataks" we suppose the relief of the country to have been modelled out during the Ice Age(s), as it is today. One of our leading geologists, Professor Høltedahl, is of opinion that we cannot do so. He calls attention to the intense erosion in the mountains at the present time, and he regards their relief to be largely of recent origin.

If such plants have not been able to migrate much from their former habitat, which they have so long occupied, we should expect to find them concentrated along or near the ancient front-line of the ice.

The available palaeontological records suggest that the mesozoic flora was very uniform. We find much the same fossils from that time in Greenland, Spitsbergen and the northernmost Arctic islands as we find southwards in temperate and warmer regions. The uniformity during the Tertiary Age was, perhaps, not so great, but it was much greater than at the present day, on account of the disturbances caused by the great glaciation. We have no palaeontological records of the Tertiary lichen flora. But there is every reason to suppose that it would have been equally uniform with the flora of Vascular plants over very wide areas.

The advancing ice must either have entirely destroyed the vegetation of the glaciated areas, driving the plants southwards, as it advanced; or there must have been refuges where a certain number of alpine Tertiary plants could have persisted, eventually other plants also that were able to accommodate themselves to the altered conditions

of life. These refuges must either have been nunataks or ice-free coasts of varying size.

If the present Arctic regions were entirely covered with a continuous ice sheet during the great Ice Age, no plants could have lived there. The entire Arctic flora of today must, in that case, have obtained its present distribution during post-glacial time. That would have necessitated long migrations from south to north, and also across the waters to Spitsbergen and to Franz Josef Land and the other isolated islands.

It seems to me that the other possibility is by far the more probable: *that at least many lichens would have persisted along ice-free coasts, and in part also on some nunataks.*

The flora of the nunataks is a very interesting problem. We have some records on the nunatak flora, but they are far from sufficient. There are the famous records from Jensen's nunatak in S. W. Greenland (63° N.), about 70–80 km. from the coast. Deichmann Branth mentions 26 species of lichens from it. In Novaya Zemlya I once climbed a nunatak east of Mashigin fjord, just south of 75° N. At the foot of the mountain, just over the glacier, I did not find a single plant. But higher up, in the upper part of the rock-fall, the vegetation considerably improved. I here found some *Drabae*, *Saxifraga cernua*, and also a considerable vegetation of mosses and lichens. The number of lichens certainly surpassed the number on Jensen's nunatak. But unfortunately a dense fog surprised me, as soon as I had reached this interesting point. I had to retire immediately, and was glad to find my tent. A fog of that kind can last for weeks on an Arctic glacier.

It is, accordingly, a well established fact that several hardy Arctic plants can live on the nunataks. Amongst the lichens I can especially mention the *Gyrophorae*, such as *G. proboscidea*, and a number of crustaceous lichens, such as *Biatorella coracina* and some *Lecideae*.

My friend P. F. Scholander worked in the North East Land of Svalbard in the summer of 1931. He promised to give as much attention as possible to the nunatak question, and we shall be glad to see his results, when published. But this low land is not so favourable for such researches as are the highlands of Spitsbergen proper and Greenland.

From what I have seen it is difficult to attribute much importance to the nunataks as refuges for Arctic plants during a heavy glaciation.

But I am quite overwhelmed with the richness of the flora of the ice-free coasts, which I have seen, even if the coast is very narrow. The necessary condition for a rich flora is that the coast is open during the breeding and hatching season of the birds. But even if there are few birds, we can find a good vegetation if the temperature during the few months of the growing season is sufficiently high, as in East Greenland.

Our meteorologists do not venture any suggestions on the temperature during the Ice Age. Our geologists have much discussed the fundamental question whether ice-free coasts really existed during the Ice Age. As far as I understand, their opinion is more and more in favour of the view that they did exist, at least during the last glaciation. Even if the traces of the ice can be seen down to the very beach in many places, there can have been an ice-free coast strip outside of the present beach, now submerged. Geologists have suggested to me that the land would have been higher—or the sea lower—during the last glaciation than today. If so the lowlands of the old ice-free coast would not be accessible to study today, a very important point.

In Greenland we have now a very severe glaciation, extending over 23 degrees, from 60°–83° N. Twenty-three degrees southwards from the Norwegian North Cape brings us down to Vienna or to Paris, far south of the old front line of the ice during the greatest glaciation. But in Greenland there are today large areas of ice-free land, about 1/7 of the whole island. We are not a little astonished to find that some of the largest of them are found along the north coast of the island, evidently on account of the low precipitation, the dry air, and consequently the great sublimation from snow and ice.

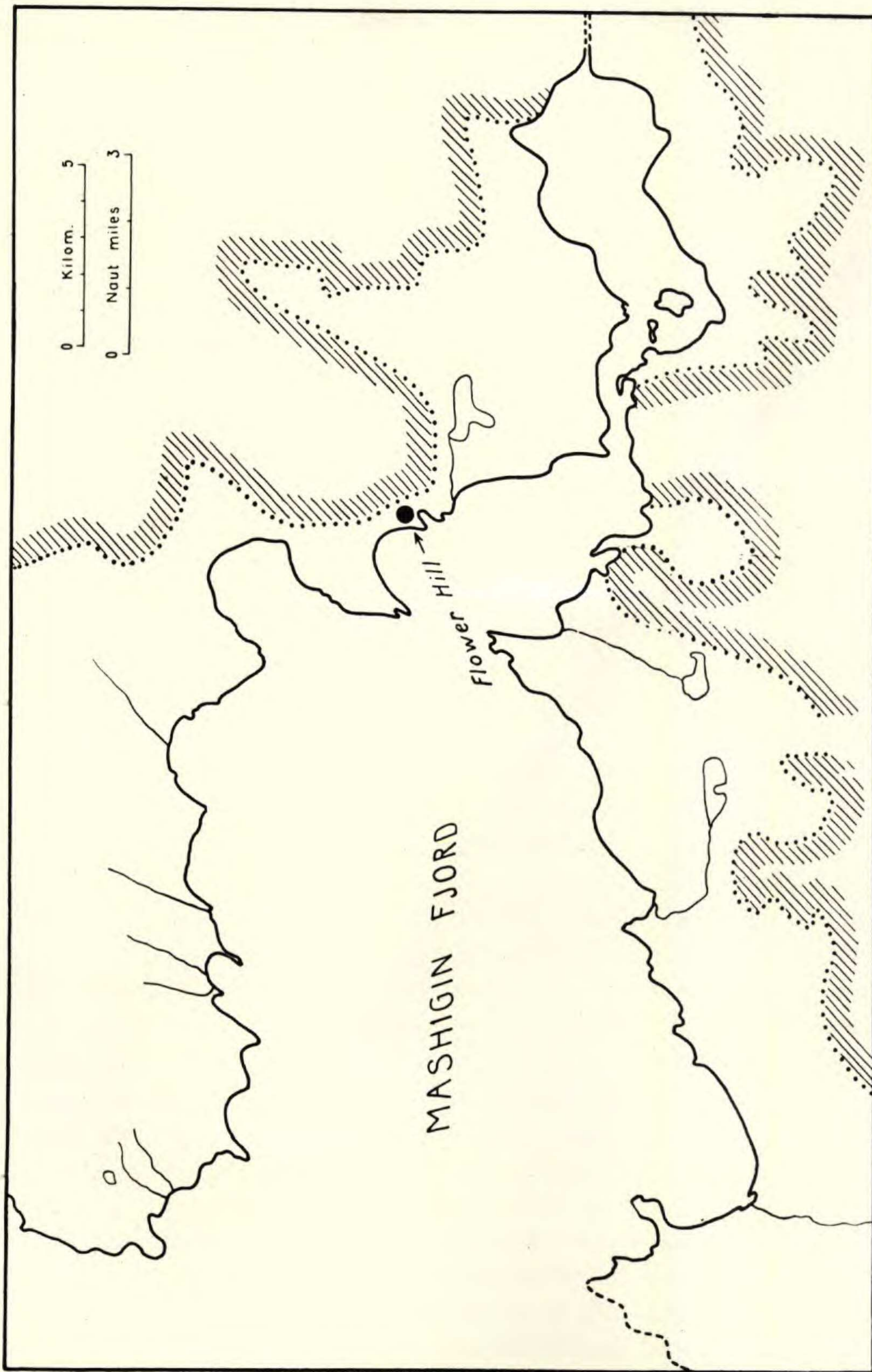
It is highly probable that we had ice-free coasts in Europe during the last glaciation, sufficient for a vegetation that was quite as rich as that of any Arctic region today. We must confess that we are less entitled to reckon upon such ice-free coasts in the present Arctic islands at the same time. But it is hardly probable that these islands would have been entirely covered with ice. A glaciation of continental extent must depend on factors of a wide range. But along the frontiers of a glaciation many local factors considerably influence the front-line of the ice. There are the dry land winds, the foehns, determined by a high atmospheric pressure over the continents. They result in a low precipitation in the lowlands, and a rather high temperature during the summer, locally limiting factors for the glaciation.

Let me devote a few words to the description of the flora of an ice-free coast. I will not describe the flora of North East Greenland, for the ice-free land is there so extensive. But in Northern Novaya Zemlya we have strips of open land, bordering large glaciated areas. I will first describe a "Flower Hill," which we found in Mashigin Fjord, Novaya Zemlya, about $74^{\circ} 40' N$. The fjord is not long, about 35 km. It is divided into three basins. The innermost of them lies in an intensely glaciated area. It is surrounded by glaciers, which here and there reach the sea. Between the glacier and the sea there is only a narrow strip of moraines with very cold, often irrigated soil, and a very meagre vegetation. But in the middle basin there is a well exposed steep hill on the north side of the fjord, which we called the Flower Hill (Norwegian "*Blomsterbakken*"). We found about 60 species of Vascular plants on this small hill. Its south side was quite covered with the most beautiful flowers seen in the Arctic (PLATE 284). There were *Cerastium Regelii*, profusely flowering, *Silene acaulis*, 3 species of *Ranunculus*, a lot of *Drabae*, 9 *Saxifragae*, luxuriant *Dryas*, 3 species of *Potentilla* in full flower, *Astragalus alpinus* and *Hedysarum obscurum*, the beautiful *Polemonium boreale*, *Myosotis alpestris* and *Eritrichium villosum*, with its flowers blue as heaven itself, *Erigeron eriocephalus* and many, many others. This Flower Hill was a revelation of beauty; where are such flowers seen, except in the Arctic?

And surrounding this splendid show of flower beauty on all sides was the glacier. Not an isolated glacier, but the mighty continental glacier itself, stretching across the island to the Kara Sea, and northwards to the very end of Novaya Zemlya. The short distance from the Flower Hill to the glacier will be seen from the sketch map (MAP 1).

The cause for this remarkable vegetation is evidently first, the position to the sun, resulting in a relatively high temperature during the summer in the soil and in the air near the soil. The well drained ground is also of high importance. This "Flower Hill" was so far from the coast that there were no bird-cliffs. The Arctic sea-birds only hatch in the cliffs close to the open sea.

We saw the influence of the birds on the vegetation in many places, but nowhere more clearly than in a great bird-cliff about $76^{\circ} N$., just south of Arkhangel Bay, in Novaya Zemlya. Though several members of our expedition had travelled much in the Arctic, not one of us had ever seen a bird-cliff of this size (PLATE 285). We regard it the greatest on the Arctic coasts. It was 200–300 meters high, and we



MAP 1. FLOWER HILL, MASHIGIN FJORD, NOVAYA ZEMLYA, SHOWING ITS PROXIMITY TO THE CONTINENTAL GLACIER.

estimated it to be about 15 km. long. The number of hatching birds was far beyond our estimate. Clouds of birds were always on the wing; thousands of birds, and thousands again, were swimming on the sea. A shot against the cliff could not fail to bring down some birds, and it scared myriads of birds to leave it, like a mighty avalanche. The sound of their wings, and of their unmelodious cries, was deafening. The odor of their excrement was penetrating.

The surroundings of this bird-cliff were the most desolate piece of land which I have ever seen in the Arctic, moist, cold clayey soil, almost destitute of plants. On a large peninsula, called Pankratyeff Peninsula, I rambled about one whole day, and only found 14-15 species of Vascular plants, the poorest result of one day's work in my Arctic experience.

But the bird-cliff itself! A continuous cover of vegetation, a soft carpet of mosses, brilliant *Caloplacae* and other lichens on the rocks, and a number of fine flowers everywhere. A lot of *Saxifragae*, of splendid development. I have never seen such plants of *Saxifraga cernua*, not even in Norway. I have never seen such plants of *Cochlearia*, mighty "cabbages" with few flowers. A goat would be highly pleased to see the meadows of *Alopecurus alpinus*, elsewhere growing as scattered individuals. There were lots of other plants, all of them profusely developed, really a "hot-bed" of great beauty. We found nearly 70 different Vascular plants on this bird-cliff. Of course my collections cannot be quite exhaustive, but the full number is not supposed to be much higher.

An enumeration of the Vascular plants from these two localities would not differ much. But the cryptogamic vegetation is very different, on account of the large number of nitrophilous lichens and mosses on the bird-cliffs, and their development to associations that cover the ground. I may refer to my paper on the lichens of Novaya Zemlya. And, like the "Flower Hill" of Mashigin fjord, the bird-cliff was surrounded by large glaciers on all sides. It was only a very narrow strip of ice-free land. Just north of it we saw the glacier-front reaching the sea for miles.

Scholander describes the same rich vegetation on the bird-cliffs of the North East Land, Svalbard, which he visited in 1931. I have also seen it on the bird-cliffs at Mitterhuken, Bell Sound, Spitsbergen. Every botanist, who has travelled in the Arctic, has seen it. It is a general feature in glaciated areas. See, for instance, the frontispiece

of Professor Seward's book, *Plant Life Through the Ages*. The author there shows us a photograph of a glacier of New Zealand, and there are tree ferns in the same photograph, growing less than 1 mile from the terminal face of the ice.

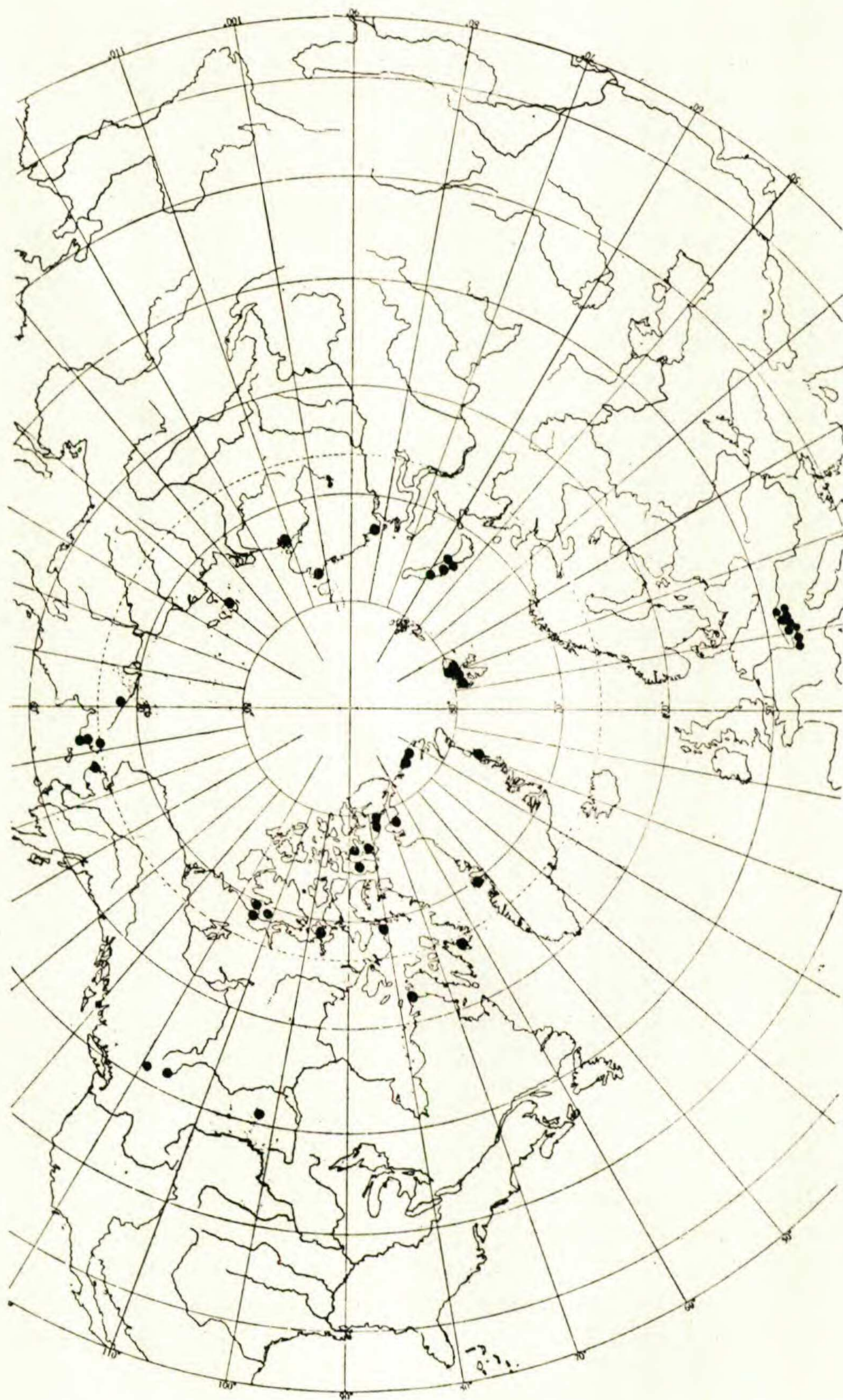
It would be of much interest to know whether there are any plants, the distribution of which is best explained if we could regard them as relic plants, living now along the borders of the old ice-sheet. It seems to me that two species of the lichen genus *Dactylina* are such plants, viz. *Dactylina ramulosa* and *D. madreporiformis*.

In Svalbard *Dactylina ramulosa* (MAP 2) is common along the north coast of Spitsbergen proper and of the North East Land. It is entirely lacking along the west coast, as well as in all the southern part of Spitsbergen. Much the same is the case in Greenland. It has repeatedly been found along the north coast, and in addition to that we have finds from Disko on the west coast (about 70° N.), and another find from Danmark Harbour on the east coast (about 76° 25' N.), but none from South Greenland.

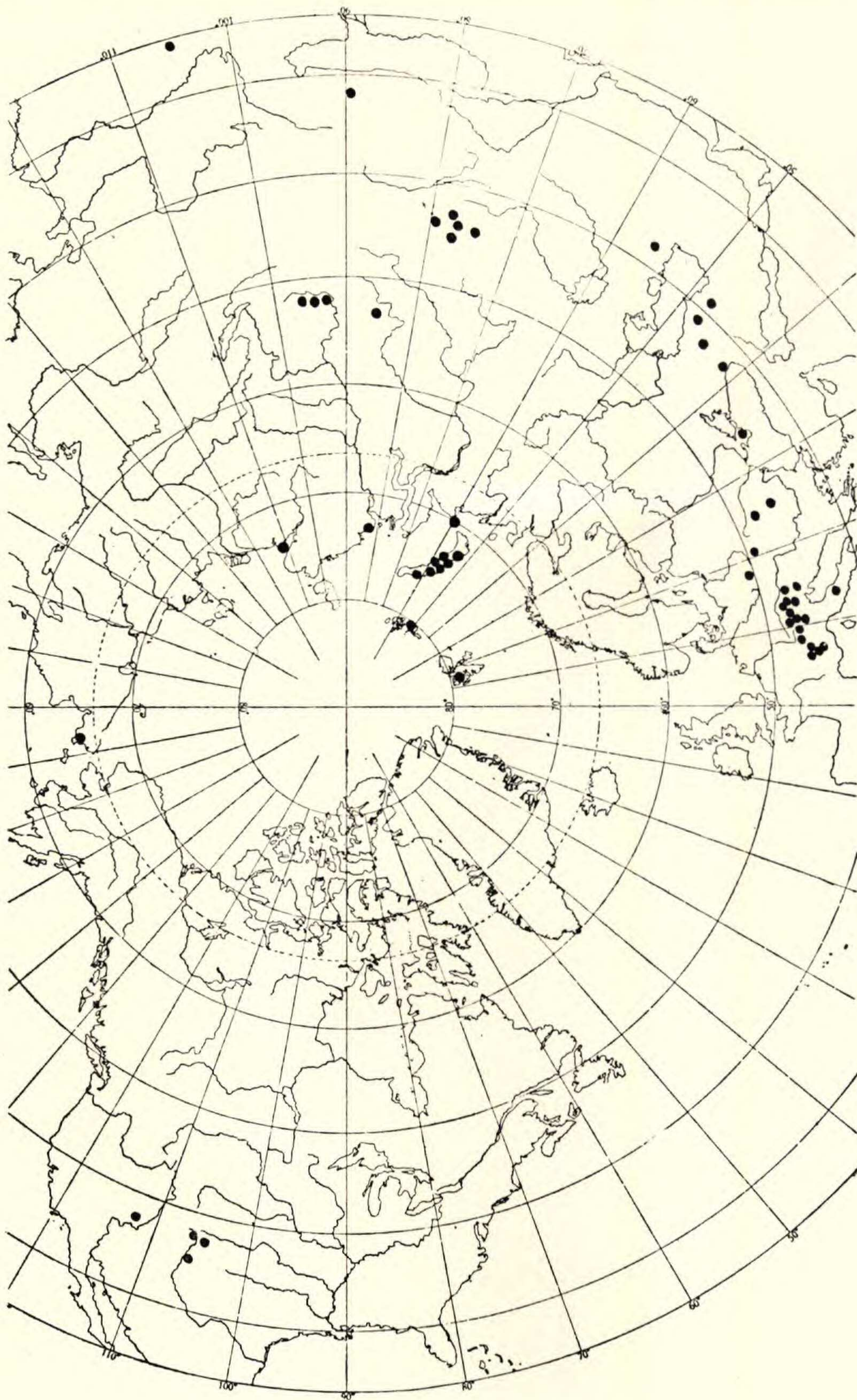
Evidently on account of the low precipitation there are large ice-free coasts in North Greenland, and much the same is the case in North Svalbard, though on a smaller scale. During the Glacial Epoch the climate must have been still more continental than at the present day, on account of the large frozen seas. It is quite possible that we have had ice-free areas, perhaps small ones, even during heavy glaciations, along the northernmost Arctic coasts. If so, we shall have to look after possible old relic plants just along the northernmost Arctic coasts, where there must have been the smallest amount of open water, also, during the Glacial Epochs.

Dactylina ramulosa is a circumpolar species, not common in Novaya Zemlya, scattered along the Siberian coast. It is much more common on the coasts of the Canadian Arctic, on the islands as well as the continent. It is entirely lacking in Fenno-Scandia, and we have no finds from Russia, and none from Siberia south of the coast. But we have several localities from the highest peaks in the Alps between Western Switzerland and Kärnthen-Steiermark. In the Rocky Mountains there are a few finds just north of the 50° parallel N. We do not know whether they are connected with the Arctic localities, for the flora of these regions is almost unknown to the lichenologists.

The other species, *Dactylina madreporiformis* (MAP 3), cannot be called circumpolar. There is only one locality, Wijde Bay, in North



MAP 2. DISTRIBUTION OF DACTYLINA RAMULOSA.



MAP 3. DISTRIBUTION OF *DACTYLINA MADREPORIFORMIS*.

Spitsbergen, but is common along the west coast of Novaya Zemlya; we have also a few finds along the Siberian coast. It is entirely lacking in Arctic America, apart from a few (not located) finds in Alaska. But we have a considerable number of localities far south in the Rockies, in Colorado, Utah and New Mexico. In the Old World it is entirely lacking in Fenno-Scandia, but it has a continuous distribution along the highest mountains from the Alps in the west over Tatra, the eastern Carpathians, the Crimea, Caucasus, Turkestan to the Sajan Mountains in the east.

Professor Helmuth Gams, the well known expert on the post-glacial history of the European vegetation, has written to me: "most of the *Dactylina* localities in the Alps are typically nunataks." Full particulars on the distribution of these two species, and a discussion of it, will be found in a paper, recently published by the present writer: "*On Dufourea and Dactylina, three Arctic Lichens*," *Skrifter om Svalbard og Ishavet*, No. 59, Oslo 1933.

If we are justified in regarding these two species as old relic plants, perhaps even of Tertiary Age, as the present author does, their history may be thus reconstructed: Very high alpine plants during the Tertiary age with its clement climate, driven to the lowland and southwards by the increasing cold and the advancing ice. Perhaps persisting along ice-free refuges along the northernmost Arctic coast down to the present day. Exterminated in Fenno-Scandia by the ice, if we can suppose that they were found here, but persisting along the mountains south of the ice-frontier. During the alternating Glacial and Interglacial Epochs there must have been considerable oscillations in the distributions of such plants, as has been pointed out *i. a.* by the English palaeontologists, Mr. and Mrs. Reid, in their well known paper: "*The Pliocene Floras of the Dutch-Prussian Border*," in *Mededeel. van de Rijksopsporing van Delfstoffen*, No. 6, The Hague 1915.

At present we are living in an Epoch corresponding to an Interglacial period, during which plants, such as the two *Dactylinas*, have to climb the highest mountains in order to find suitable localities. It is, therefore, only to be expected that they should be restricted to the highest Alps in Central Europe, down to about 1800 meters above sea-level.

But why are they lacking in the Scandinavian mountains where excellent localities are so abundant? It is hard to explain. We do

not know whether they have ever been there. But let us suppose that they have. It is possible that the greatest glaciation was so complete that it destroyed all vegetation, and that the two *Dactylinas* have not been able to immigrate since that time. As far as I understand, geologists are of opinion that at the beginning of the Interglacial Epochs temperature must have risen considerably, and during relatively brief periods (geologically speaking) have attained heights which made successful attacks on the mighty ice-cap possible.

It is not every species of plants which is able to migrate so easily that it can profit from the possibilities offered by rapidly retiring ice. On the contrary, we find that a great number of the plants which we know to be relic, for the reason that we know their geological history as well as their present distribution, have a very reduced power of distribution. Numerous such cases are so well known that it is unnecessary for us to give particulars in this brief summary. It is sufficient to refer to Professor M. L. Fernald's papers on the persistence of plants. The present distribution of *Dactylina ramulosa* in the Svalbard region suggests a species with a very reduced power of migration. Its distribution in the Alps and also the widely scattered areas of *Dufourea madreporiformis* likewise suggest a reduction of capacity to migrate.

It will be seen that the study of Arctic botany brings before us problems of a very general character. One of them, the eventual persistence of plants, Arctic as well as others, can with great advantage be attacked by a careful study of the vegetation along the border line of the old glaciations. In America we have the classical studies by Professor Fernald on the persistence of Vascular plants. It is much to be desired that his work should be followed by investigations on the lichen vegetation of the high Rocky Mountains on either side of the old "ice-line." No other group of plants can throw more light on this great problem than the lichens which can grow in profusion close to the mightiest glaciers.

EXPLANATION OF PLATES

PLATE 284. Dense Vegetation of "Flower Hill," Mashigin Bay, Novaya Zemlya (see location on MAP 1): *MYOSOTIS ALPESTRIS*, *ERIGERON ERIOCEPHALUS*, *TARAXACUM* SP., *ASTRAGALUS ALPINUS*, *POLYGONUM VIVIPARUM*, etc. *Photo. B. Lynge*, August 4, 1921.

PLATE 285. Part of the bird cliff south of Arkhangel Bay, Novaya Zemlya, with myriads of *URIA LOMVIA* and other birds. *Photo. B. Lynge*, August 12, 1921.

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